# *HEXAPHYLLIA*: A SPINY HETEROCORAL FROM LOWER CARBONIFEROUS REEF LIMESTONES IN DERBYSHIRE, ENGLAND

by PATRICK J. COSSEY

ABSTRACT. Exceptionally well preserved and abundant corallites of *Hexaphyllia* are recorded from limestones of the Lower Carboniferous Castleton Reef Belt, north Derbyshire, UK. Details of corallite morphogenesis are presented and the growth attitude of corallites is determined. Tabulae curve down at their margins and fuse together to form the tabulotheca. Conversely, spines curve upward and point in the direction of corallite growth. Soft tissue reconstructions infer the presence of polyps sitting exposed upon and totally enclosing the distal tips of the corallites, with polyp lobes extending down their sides. Much of the corallite is therefore regarded as endoskeletal in origin. Rows of spines projecting from between the polyp lobes gave some degree of protection to the exposed polyps. Assemblages of corallites from different positions in the reef show notable differences in morphology. Variations in shape, wall thickness and tabulae spacing are attributed to contrasting growth rates at different positions within the reef. Examination of approximately 1300 corallites from two localities in the reef reveals the presence of a single species, *Hexaphyllia marginata* (Fleming), which shows considerable intraspecific variation. Systematic studies indicate that criteria used to distinguish *Hexaphyllia* species in the past are invalid and that the majority of previously described taxa are junior synonyms of *H. marginata*. Heterocoral mode of life is discussed in the light of observations made on this species.

THE heterocorals are a very unusual and highly distinctive coral group ranging from the Lower Devonian to the Upper Carboniferous. Typically solitary, but rarely weakly colonial, their ontogeny is characterized by unique methods of wall formation and septal insertion. Corallites were elongate and are commonly preserved only as short fragments. The tabulae which are well-spaced in the axial region of the corallite, bend through an angle of almost 90° towards the corallite edge, thicken, and fuse to form the wall between the peripheral edges of the similarly thickened septa. The septa commonly project through the wall and form longitudinal ridges or costae on the external surfaces of corallites. These may occasionally be adorned with a delicate ornament of spines or tubercles (Text-fig. 1). Although relatively uncommon during the earlier part of their range, the distribution of heterocorals during the early Carboniferous was world-wide. They are particularly well known in Europe and south-east Asia, and specimens are found in a wide variety of sedimentary facies. Heterocorals are also common in some reef limestones (Mundy *in* Ramsbottom 1978; Mundy 1980; Cossey 1983; Sugiyama 1984). Although Schindewolf (1941) originally suggested that they led a pseudoplanktic existence attached to seaweeds, more recent work indicates that the heterocorals were benthic sessile forms during their adult life (Rózkowska 1969; Cossey 1983; Sugiyama 1989; Weyer 1995*a*, 1995*b*). However, further work on heterocoral ecology and mode of life will be required before the group is to be fully understood.

The first appearance of heterocorals in the stratigraphical record is that of *Tetraphyllia devonica* described by Yoh *et al.* (1984) from the Lower Devonian (Emsian) of south-eastern Yunnan, China. Recently, however, Tourneur and Herrmann (in press) questioned the systematic affinity of *T. devonica* and suggested that their own discovery of *Stellaphyllia* from Mid Devonian (Eifelian) strata in the Cantabrian Mountains of northern Spain represents the earliest heterocoral on record. Other significant Devonian occurrences are from the Upper Devonian, with the appearance of *Oligophylloides* and *Mariaephyllia* (Famennian) in the Holy Cross Mountains in Poland
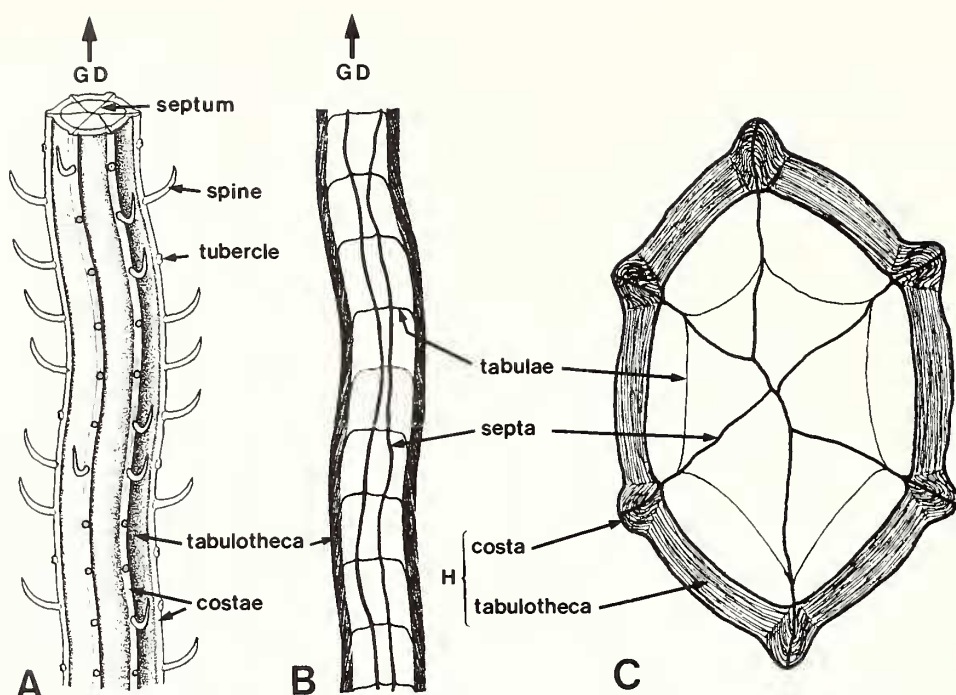
TEXT-FIG. 1. Heterocoral morphology as typified by *Hexaphyllia*. A–B show corallites reconstructed with spines and tabulae in their correct orientation with respect to the growth direction. A, external view of corallite. B, longitudinal section. C, transverse section. GD, growth direction; H, heterotheca.

(Rózkowska 1969), Morocco and the Rheinisches Schiefergebirge, Upper Franconia and Thuringia in Germany (Weyer 1995*a*). Heterocoral diversity and abundance increased in the early Carboniferous, with the early introduction of *Hexaphyllia* and *Heterophyllia* in the late Tournaisian–early Viséan, but it was not until the Asbian that the heterocorals reached their acme (Sutherland and Mitchell 1980; Cossey 1983). Records of both *Heterophyllia* and *Hexaphyllia* continue in the Upper Carboniferous (Wilson 1960; Perret and Vachard 1977; Igo and Kobayashi 1980; Sutherland and Mitchell 1980; Lin and Peng 1990; Weyer and Polyakova 1995) along with *Anomalophyllia* (Tourneur *et al.* in press), until the group finally became extinct part way through the Namurian, during the Chokierian – H_1 Zone (Metcalfe *et al.* 1980). Further details of the geographical and stratigraphical distribution of heterocorals are detailed in Weyer (1967), Sutherland and Mitchell (1980), Wang (1980), Cossey (1983), Poty (1983) and Sugiyama (1984).

The systematic position of the group has for a long time been uncertain. Early workers regarded the heterocorals as belonging either to the Rugosa (Roemer 1880; Thomson 1883; Neumayr 1889; von Zittel 1924) or the Scleractinia (Duncan 1867; Stuckenberg 1904), but others were less sure (M'Coy 1851; Milne Edwards and Haime 1852; Kunth 1869; Carruthers *in* Lee 1909; Hill 1938–41, 1956). Later work on septal insertion patterns led Schindewolf (1941) to conclude that the heterocorals were of neither rugosan nor scleractinian affinity and a new order was established for the group, namely Heterocorallia.

Many different models of septal insertion for the group have been suggested (Yabe and Sugiyama 1940; Poty 1978*a*, 1978*b*, 1981; Lafuste 1979; Sutherland and Forbes 1980; Sugiyama 1984; Fedorowski 1991) and details of heterocoral microstructure are well known (Lafuste 1981, 1987; Karwowski and Wrzolek 1985, 1987; Wang 1988; Rodriguez 1989; Wang *et al.* 1989). Despite this,

the relationship of Heterocorallia to other coral groups is still unknown. Similarities in the morphology of *Oligophylloides* and the rugosan *Pseudopetraia* led Hill (1981) to suggest that Heterocorallia may have evolved from a rugose coral stock in the Devonian. This theme was further developed by Fedorowski (1991, 1993) who suggested that Heterocorallia be placed alongside a new order, Calyxocorallia (containing *Pseudopetraia*), in a major new cnidarian subclass, Dividocorallia. This view was subsequently challenged by Wrzolek (1993*a*) who argued that since critical septal insertion evidence is lacking in Fedorowski's (1991) account, the phylogenetic relationship between Heterocorallia and Rugosa must remain unclear.

In Europe, only four well-established heterocoral genera are known. These are *Hexaphyllia* Stuckenberg, 1904 – heterocorals with only six septa, based on material from Russia and Scotland; the thicker walled, multiseptate forms *Mariaephyllia* Fedorowski, 1991 and *Oligophylloides* Rozkowska, 1969 – both from Germany and Poland; and *Heterophyllia* M'Coy, 1849 – based on material from Derbyshire. The great morphological variation in heterocoral populations was first appreciated by Young (1868, 1869) who, in a meticulous study of material from Scotland, clearly demonstrated the synonymy of *Heterophyllia mirabilis* and *H. lyelli*, two species that were originally described by Duncan (1867) and later transferred to *Hexaphyllia* by Stuckenberg (1904) and Robinson (1917). Sadly Young's pioneering work was criticized by established authorities at the time and its significance with respect to heterocoral research has largely gone unrecognized. Further details of intraspecific variation in heterocoral populations have been recorded, most notably in *Hexaphyllia* (Poty 1978*a*, 1981; Sugiyama 1984; Herbig 1986; Rodriguez and Comas-Rengifo 1989), but the relevance of this work to species definition in *Hexaphyllia* has yet to be fully evaluated.

In recent years many new heterocoral taxa have been described from south-east Asia, including more than 40 new species of *Hexaphyllia* from various parts of China (Jia and Xu 1975; Jia *et al.* 1977; Yu *et al.* 1978; Wang 1980; Xu 1981; Wang and Ye 1984; Lin and Wu 1985; Huang and Ma 1986; Lin *et al.* 1992; Liu and Su 1992; Lin and Yuan 1994). So far, few have questioned the validity of these new taxa, but, as Fontaine *et al.* (1991) suggested, probably far more species of *Hexaphyllia* have been described than are actually represented by the material. Concerns expressed by Rodriguez and Comas-Rengifo (1989) and Fedorowski (1991) regarding the validity of *Hexaphyllia* indicate that a review of the genus is long overdue.

Although general aspects of heterocoral morphogenesis are well known (Fedorowski 1991), our detailed understanding of corallite development and growth direction stems largely from work on the genus *Oligophylloides* (Rózkowska 1969; Sutherland and Mitchell 1980; Wrzolek 1980, 1993*b*). Comparable studies of other heterocoral genera have not hitherto been published. This paper considers the morphogenesis, systematics and palaeoecology of *Hexaphyllia* and is based on by far the richest and best preserved heterocoral fauna so far discovered in England. Exceptional preservation has facilitated a reconstruction of the *Hexaphyllia* polyp and, for the first time, spine orientation is defined in relation to corallite growth in both *Heterophyllia* and *Hexaphyllia*. The present paper is based on the observation of approximately 1300 corallites observed in hand specimen (42 per cent.), peel section (51 per cent.), and thin section (7 per cent.).

LOCATION AND FIELD OBSERVATIONS

The heterocorals which form the basis of this account are of early Carboniferous (Asbian) age and originate from two localities in Upper B_2 reef limestones of the Castleton Reef Belt, north Derbyshire (Text-fig. 2). Locality A (SK 13758270) is situated in fore-reef limestones near Winnats Pass and Locality B (SK 13478302) occurs in limestones of the algal reef complex at the top of Treak Cliff (Wolfenden 1958; Stevenson and Gaunt 1971; Broadhurst and Simpson 1973). Although the exact age equivalence of the two localities cannot be demonstrated (see discussion in Cossey 1983), their contemporaneity is assumed in this account. Records of heterocorals are also known from the
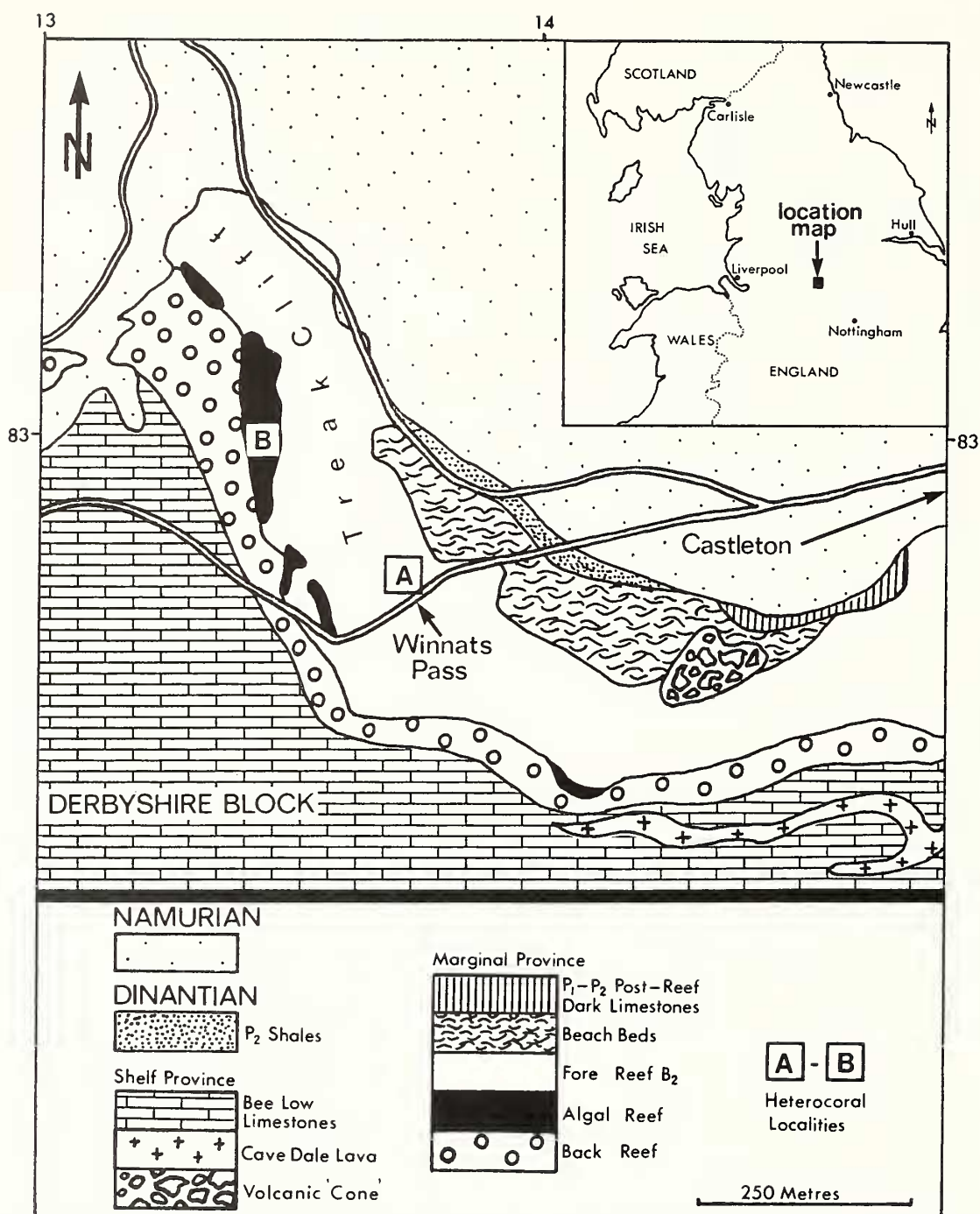
TEXT-FIG. 2. Geology of the Castleton Reef Belt in north Derbyshire indicating the position of heterocoral localities referred to in the text (modified after Stevenson and Gaunt 1971; Cheshire and Bell 1977).

shelf province Bee Low Limestones (the lateral equivalent of the Castleton Reef Belt deposits) but are uncommon (Cossey 1983). Further details concerning the stratigraphy and palaeoecology of the Castleton Reef Belt have been documented by Parkinson (1965) and Timms (1978).

Locality A. The heterocorals occur in fossiliferous, bedded limestones, which Stevenson and Gaunt (1971) recognized as characteristic of their fore-reef facies. The material consists of over 1100, exceptionally well preserved corallites of *Hexaphyllia* concentrated in thin layers, up to 10 mm thick (Pl. 1). Most corallites were found oriented in a subparallel position with respect to each other and lying with their long axes in the plane of the bedding. Some corallites oriented at an angle to the bedding and with spines curving upwards appeared to be in life position. These features suggest that the corallites may have been 'nesting' in a relatively protected niche within the fore-reef and subsequently concentrated in layers by winnowing, either as result of current activity, or by wave/storm surge. The associated fauna is dominated by the disarticulated, colour-banded, pectenoid bivalve *Streblochondria elliptica* (Phillips), described in detail by Shaw (1970), buxtoniid brachiopods, delicate fenestrate bryozoans and goniatites (see Text-fig. 12).

The preservation of so many corallites from this locality is attributed to the early formation of a radiaxial fibrous mosaic (Bathurst 1971). Unfortunately however, the development of this neomorphic fabric (Kendall and Tucker 1973) has resulted in the modification of primary textures to such an extent that details of the corals' microstructure and of the original sediment matrix are largely indeterminable (Cossey 1983; and see Pl. 2, fig. 1; Pl. 3, fig. 7).

Locality B. The heterocorals occur in massive fine-grained micritic limestones and are associated with limestones from which Wolfenden (1958) described stromatolites of the *Collenia-Cryptozoon* type. Stevenson and Gaunt (1971) later referred to these deposits as of 'algal reef' facies. The material from this locality includes approximately 200 *Hexaphyllia* corallites, many with tubercles, but only a few with spines, and a solitary specimen of *Heterophyllia ornata* M'Coy, also with spines (Pl. 2, fig. 8). The majority of corallites were found lying prone and with their long axes oriented subparallel to the strike of the reef crest. These features suggest that corallites were transported a short distance from their growth position by currents prior to deposition and that during this time their spines were removed by mechanical abrasion. The associated fauna is dominated by *in situ* colonies of *Siphonodendron* spp. (see Text-fig. 13). Although neomorphic effects have also modified the sediment fabric from this locality, the original limestone appears to have been either a biomicrite or a poorly washed biosparite.

Further details of the taphonomy and palaeoecology of the assemblages are given by Cossey (1983), complete with faunal lists from both localities.

MORPHOLOGY

Early growth and orientation

Details of the early ontogeny in heterocorals are scarce since corallites are usually found as small, solitary, fragmented lengths and juvenile corallites are rare. Defining the growth direction of corallites has also proved difficult for, as reference to the literature indicates, heterocorals have been figured in completely different orientations, by various authors. However, a clearer view of heterocoral growth has emerged in recent years with the discovery of what has been widely regarded as weakly colonial coralla in which juvenile offsets have been observed branching away from larger adult corallites (Weyer 1995b; Tourneur *et al.* in press; Tourneur and Herrmann in press). Studies of *Oligophylloides* by Rózkowsa (1969) and Wrzolek (1980), for example, indicate that juvenile corallites developed broad bases where they connected with the adult corallites, and that the tabulae curved peripherally downwards in relation to the growth direction as they fused to form the wall.
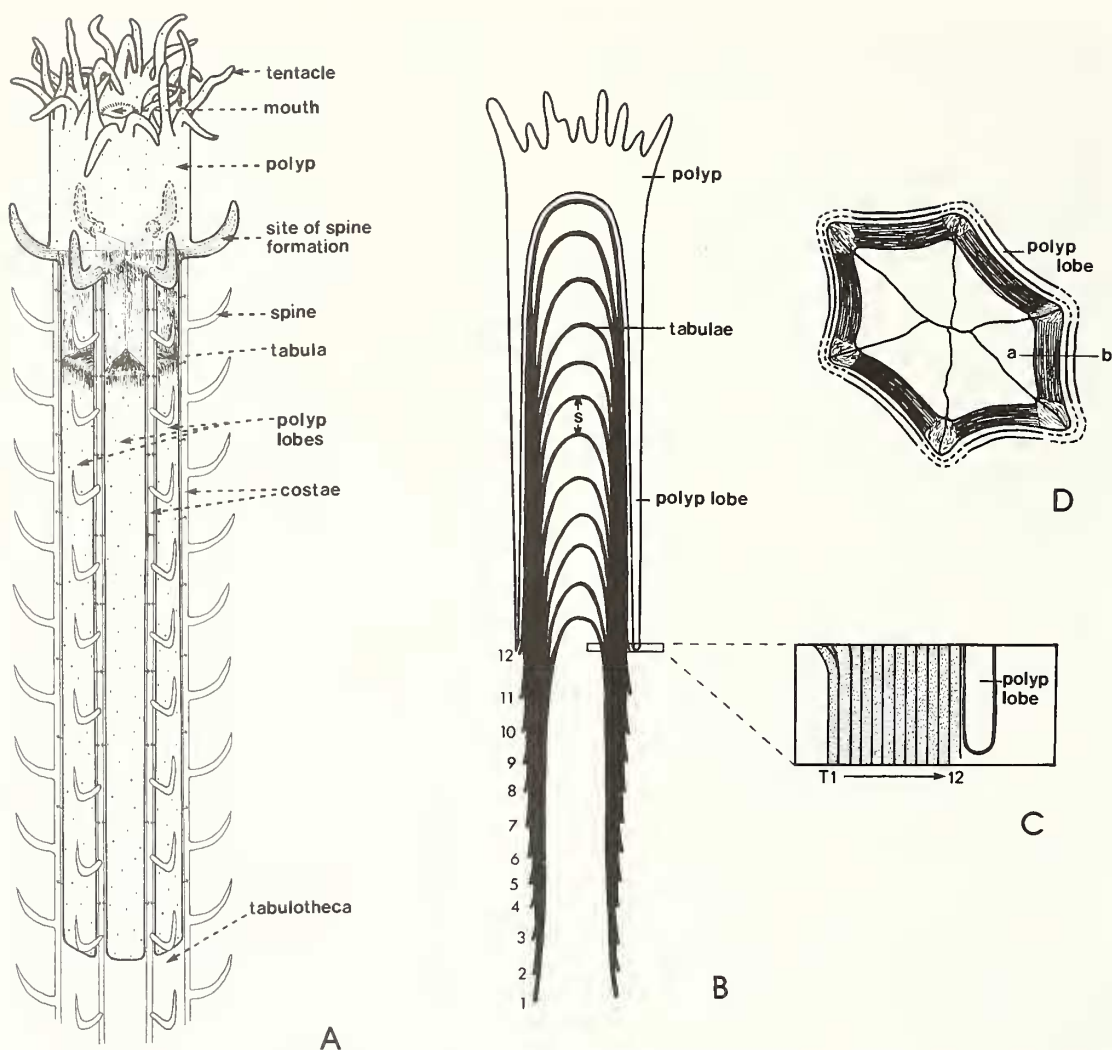
TEXT-FIG. 3. Polyp reconstruction. A, *Hexaphyllia* corallite with polyp in life position. Note the development of polyp lobes extending down the outside of the corallite and the presumed site of spine formation near the top of the polyp. B–D, determination of polyp lobe length in *Hexaphyllia*. The length of the polyp lobes is derived by multiplying the tabulae spacing distance (s) by 11 (see text for further explanation). B, longitudinal sketch section through polyp and corallite. C, enlarged part of B showing 12 fused tabulae (T1–12) in the wall structure. D, cross section of corallite illustrating the lamellar fabric of the wall resulting from the peripheral fusion of the tabulae (a–b = line of the section illustrated in C).

EXPLANATION OF PLATE 1

Figs 1–8. *Hexaphyllia marginata* (Fleming, 1828); Winnats Pass (locality A), Castleton Reef Belt, Derbyshire; all from Upper B_2 (Asbian) fore-reef limestones. Figs 2 and 5–7 illustrate the attachment of juveniles to adult corallites and in fig. 8, the relationship between spine and tabulae can be discerned. 1, MM LL10919; × 3. 2, MM LL10911; × 3. 3, MM LL10920; × 5. 4, MM LL10919; × 9. 5, MM LL10911; × 7. 6, MM LL10912; × 7. 7, MM LL10910; × 8. 8, MM LL10920; × 13.

PLATE 1
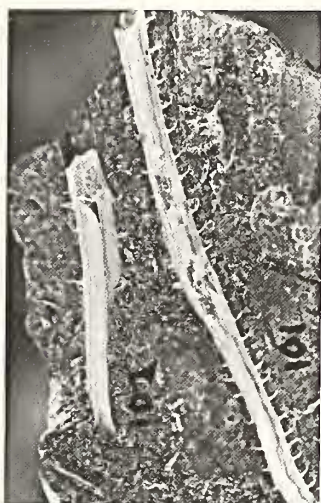
COSSEY, *Hexaphyllia*

Branching of this kind has also been observed in *Heterophyllia* by Duncan (1867, pl. 31, fig. 6a) and in *Radiciphyllia* by Sugiyama (1984, pl. 7, fig. 1b; text-fig. 17). In these examples, evidence that the developing offsets originated from the parent corallites to which they are attached is obvious, since the morphology of the adult is usually strongly modified in the zone of contact between them.

So-called 'branching phenomena' may also be recognized in the present account (Pl. 1, fig. 2) but evidence that the juvenile offsets arose from the subdivision of adults by an asexual budding process is difficult to prove. Here, the angle of divergence between juvenile and adult is quite variable and occasionally two offsets diverge from a 'parent' in different directions (Pl. 1, figs 5–6). In addition, there is no obvious change in the morphology of the adult at its contact with the juvenile (Pl. 2, figs 3, 5–6; Pl. 3, figs 2, 4), the contact surface between juvenile and adult is extensive, and the spines of adult corallites are sometimes enveloped by the offsets (Pl. 1, figs 5, 7; Pl. 2, fig. 6). These features suggest that the relationship between the juvenile and adult corallite is more likely to have developed as a result of an encrustation process rather than from budding. In such examples the juvenile corallites would clearly represent the very earliest stages in corallite development formed after the settlement of planula larvae on the adult corallite substrates, their broad expanded bases forming 'talons' analogous to those described in other heterocoral genera by Rózkowska (1969) and Wrzolek (1980). This conclusion does not, however, preclude the existence of budding in *Hexaphyllia*; it merely draws attention to the difficulty in distinguishing between the phenomenon of branching by asexual budding from that of attachment by larval encrustation.

Regardless of their origin, such associations between young and adult corallites have enabled the direction of tabulae curvature to be fixed in relation to the growth direction. The tabulae which are widely spaced along the corallite axis curve peripherally downwards in the opposite direction to that of corallite growth (Pl. 2, figs 3, 5–6). In hand specimen (Pl. 1, fig. 8) and in thin section (Pl. 2, figs 6–7), spines were observed curving consistently in the opposite sense to that of the tabulae and pointing upwards in the direction of corallite growth. A similar relationship between tabulae and spines was also noted in *Heterophyllia* (Pl. 2, fig. 8) in which spines are recorded for the first time (and see Pl. 3, fig. 1). Text-figure 1A–B illustrates the correct orientation of *Hexaphyllia* in it life position.

Details of septal insertion are difficult to establish, since insertion was initially extremely rapid and subsequently very slow. Either four or five septa appear in some corallites before they have reached 4 mm in length (Pl. 2, fig. 5; Pl. 3, fig. 2). In some corallites as few as three septa occur (Pl. 3, fig. 9).

EXPLANATION OF PLATE 2

Figs 1–8. Heterocorals from the Lower Carboniferous, Castleton Reef Belt in North Derbyshire. All specimens are of Upper B$_2$ (Asbian) age.

Figs 1–7, *Hexaphyllia marginata* (Fleming, 1828). 1–3, 5–7, from the fore-reef at Winnats Pass (locality A). 4, from the algal reef at Treak Cliff (locality B). Figs 1–2 and 4 show the development of tabulae in the wall structure. 1, transverse thin section, MM LL10907b; × 47. 2, transverse thin section, MM LL 10908; × 38. 4, transverse peel section, MM LL10900a; × 39. Figs 3, 5–6 show young corallites growing away from adult corallites to which they are attached. From such specimens the curvature of the tabulae may be fixed in relation to the growth direction. 3, transverse peel section, MM LL10909k; × 9. 5, transverse peel section, MM LL10909aa; × 15. 6, transverse peel section, MM LL10909d; × 14. Figs 6–7 illustrate the relationship between spine curvature and tabulae curvature. 7, transverse peel-section, MM LL10906a; × 14.

Fig. 8. *Heterophyllia ornata* M'Coy, 1844; MM LL10900e; algal reef at Treak Cliff (locality B). Note that the relationship between spine curvature and tabulae curvature is the same as that in figures 6–7; longitudinal peel-section; × 15.

PLATE 2

COSSEY, *Hexaphyllia*, *Heterophyllia*
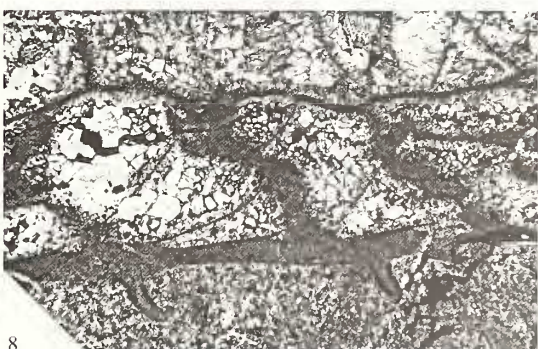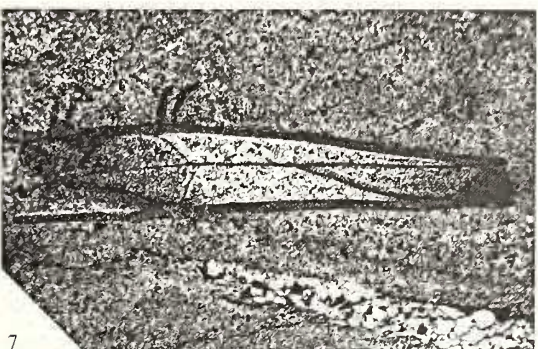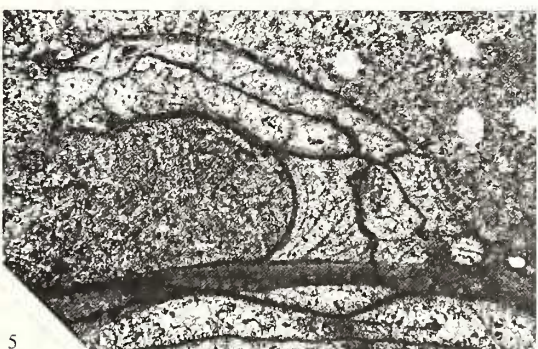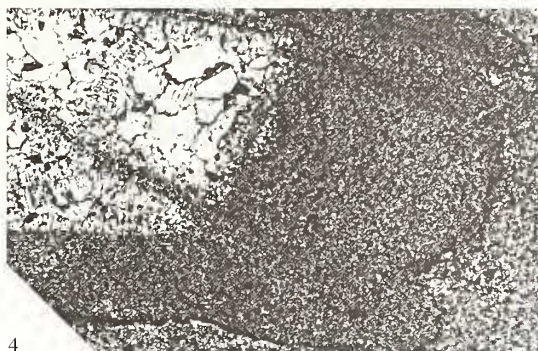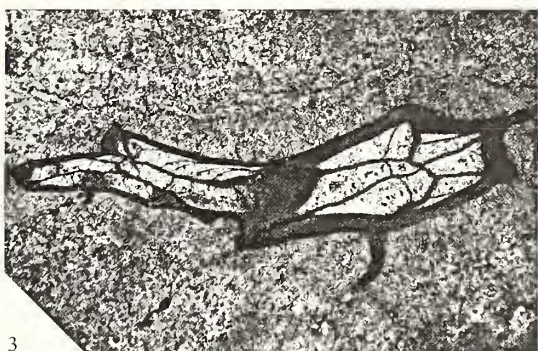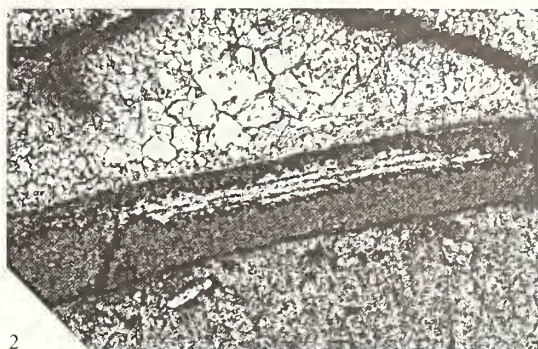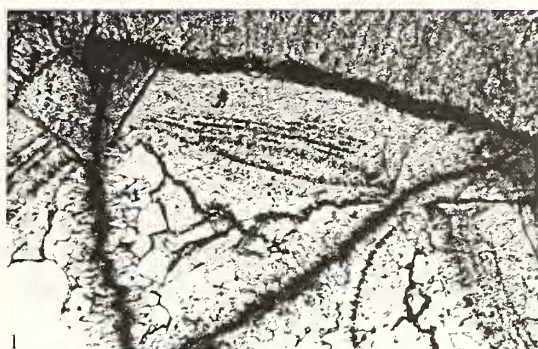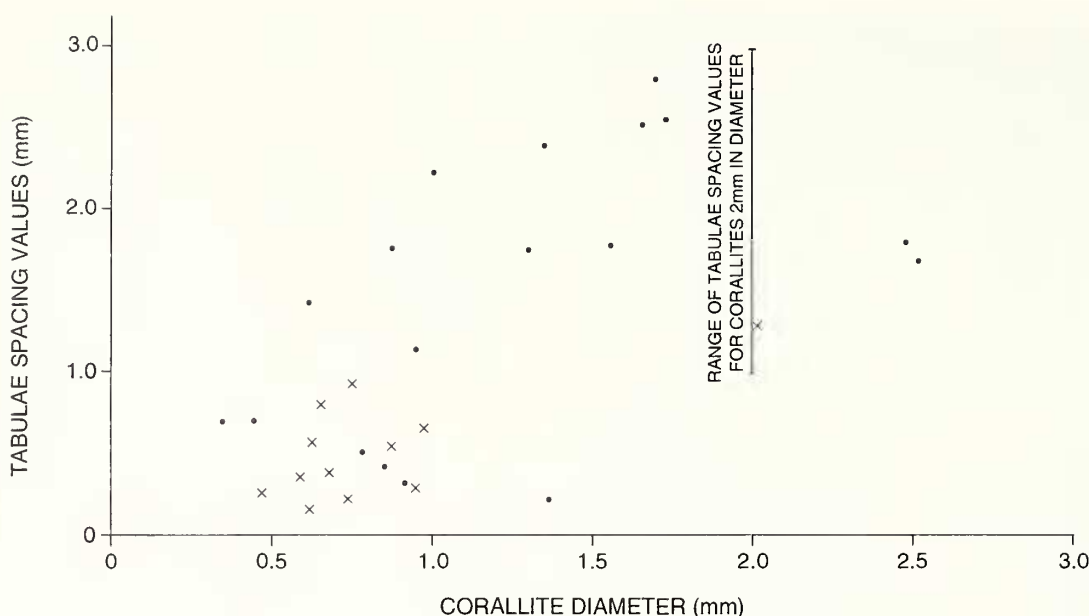
TEXT-FIG. 4. The relationship between corallite diameter and tabulae spacing in *Hexaphyllia marginata* (Fleming, 1828). Dots represent corallites from the fore-reef (locality A) and crosses corallites from the algal reef (locality B). Note that for corallites 2 mm in diameter the tabulae spacing value ranges from approximately 1–3 mm.

Reconstruction of the polyp

It now seems likely that in all heterocoral genera the tabulae curve peripherally downwards away from the corallite axis before fusing to form the corallite wall (Wrzolek 1980; Cossey 1983; Fedorowski 1991). The implication of this unique method of wall formation is significant in that the corals would have lacked a protective cup-like calyx. Furthermore, polyps would have sat exposed upon the tapered growing ends of corallites (referred to as distal cones by Wrzolek 1980, 1993b) and with soft polyp tissue extending down the outside of the corallite forming the wall (the tabulotheca). The corallites were therefore largely endoskeletal in origin. In *Hexaphyllia*, the expanded peripheral ends of the septa commonly project beyond the outer edges of the tabulotheca to form the costae and spines. In order to allow for the secretion of the tabulotheca, it is necessary to invoke the presence of up to six polyp lobes extending down the outside of the corallites between the costae (Text-fig. 3A–B). Clearly, the exposed polyps would have been extremely vulnerable to attack from predators were it not for the presence between the polyp lobes of upward curving spines. Protection is therefore seen as the primary function of the spines. For further details relating to the secretion of spines and costae, see Cossey (1983).

The extent to which corallites were enclosed by the polyps and the length of polyp lobes can easily be determined, if only by indirect means. Wrzolek (1993b) used trigonometry to calculate the height of the distal cone in heterocorals using the apical angle (the angle between the corallite axis and the peripheral edges of the tabulae) and the vertical separation distance of the tabulae at the corallite axis. The height of the distal cone corresponds exactly to the length of corallite enclosed and thus directly to the length of the polyp lobes. Figures were obtained by Wrzolek (1993b) for *Oligophylloides*, *Heterophyllia*, *Longlinophyllia* and *Hexaphyllia* of 2–188 mm, 7 mm, 7 mm and 11 mm respectively. Another convenient method of calculating the polyp lobe length and the method used here, uses the number of tabulae fused in the wall at any given level in the corallite

TEXT-FIG. 5. Determination of polyp lobe length in *Hexaphyllia*. A, based on a spacing of 1 mm between tabulae. B, based on a spacing of 2 mm between tabulae. C, based on a spacing of 3 mm between tabulae. P, polyp; PL, polyp lobes; S, septa; T, tabula; W, wall.
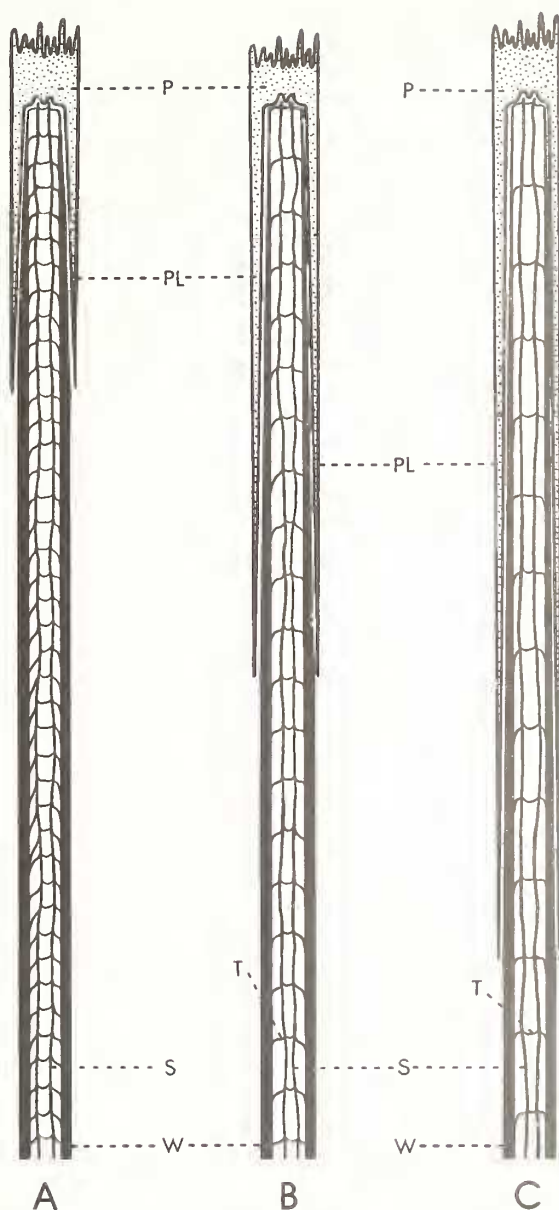
and the average tabulae spacing value at the corallite axis (Cossey 1983). Detailed observations of *Hexaphyllia* corallites seen in thin section (Pl. 2, figs 1–2, 4) indicate that for corallites approximately 2 mm in diameter the established number of fused tabulae in the tabulotheca is 12. Reference to Text-figure 3B–D indicates that for such corallites the polyp lobe length must equate to the distance between the corresponding 12 tabulae at the corallite axis or 11 times the average distance between tabulae. Text-figure 4 indicates that in corallites of 2 mm diameter the average tabulae spacing value ranges from 1–3 mm. Accordingly, the length of polyp lobes in *Hexaphyllia* can be calculated as 11–33 mm (Text-fig. 5).

The existence of polyp lobes and their progressive movement up the sides of corallites during growth can be envisaged from Text-figure 11A, where the component tabulae in the wall structure may be seen overlapping one another like slates on a roof.

Morphometrics

Wall shape and thickness. The shape of any corallite is determined by the shape of its wall. Wall shape can be defined by two ratios. The inner wall shape ratio defines the shape of the inner wall, whilst the outer wall shape ratio defines the shape of the outer wall. In each case, the number of wall-sections that are respectively convex (Cx), flat (F) and concave (Ce) is expressed by the ratio Cx:F:Ce. Text-figure 6 indicates how wall shape ratios are determined and how pyramid diagrams can be used to define different corallite shapes. Definition of wall shape ratios for the Castleton material indicate that the shape of *Hexaphyllia* corallites from both localities in the reef belt is continuously and widely variable (Text-fig. 7). Although cylindrical, prismatic and stellate corallite shapes were found at both localities, cylindrical forms were more prevalent in the algal reef and stellate forms more common in the fore-reef (Pl. 3, figs 14–15). Where cylindrical forms are present the inner walls are commonly more convex than the outer walls. This suggests that cylindrical forms were not the product of corallite abrasion prior to burial.

Variations in wall thickness were also noted between the two localities. Text-figure 8 indicates that wall thickness increased as corallites grew larger and that individuals from the algal reef developed slightly thicker walls than those from the fore-reef.

If (as discussed earlier) the age equivalence of the two localities is assumed, then the functional significance of these morphological variations is striking. The thicker-walled and relatively robust, cylindrical corallites from the algal reef were better suited to life in more turbulent, shallow water close to the reef crest while the more delicate, thinner-walled, stellate corallites are more likely to have lived at greater depths on the fore-reef in less turbulent conditions.

Corallite diameter. Size-frequency plots indicate a wide but continuous range in corallite diameter for *Hexaphyllia* corallites at both localities in the reef belt (Text-fig. 9). In each case the range in corallite diameter is broadly similar, but specimens from the fore-reef have a slightly greater range (0·1–2·6 mm) than those of the algal reef (0·2–2·2 mm). A normal size distribution is indicated in the plots from the fore-reef. The plot for individuals with six septa from the algal reef shows a pronounced bimodal distribution with two prominent peaks, occurring at the 0·9 mm and 1·7 mm corallite diameter marks respectively. The gap between these two peaks represents an absence of corallites with a diameter of 1·2–1·3 mm. Various explanations for this bimodal distribution were suggested by Cossey (1983), including: the presence of more than one corallite generation; the presence of more than one species; the selective removal of the 1·2–1·3 mm diameter corallites; and rapid growth through the 1·2–1·3 mm size range producing corallites with short, tapered sections along their length.

Although the last hypothesis was originally favoured by Cossey (1983), it is now regarded as an unlikely explanation for the bimodality described, since corallites in the 1·2–1·3 mm diameter range are now known to occur (from locality A described here, and see Poty 1978a, 1981; Herbig 1986; Rodriguez and Comas-Rengifo 1989) and in none of these cases has a corallite showing tapered growth been directly observed. Bimodal distributions in other heterocoral assemblages have, however, been recorded and these have been interpreted as indicating the presence of more than one species (Poty 1978a, 1981). In such examples, morphological differences other than corallite diameter are used to support the argument. Since no other morphological differences were noted in corallites from the algal reef, the presence of more than one species is unlikely to be the cause of the bimodality described. Bimodality arising from the presence of two generations is also doubted
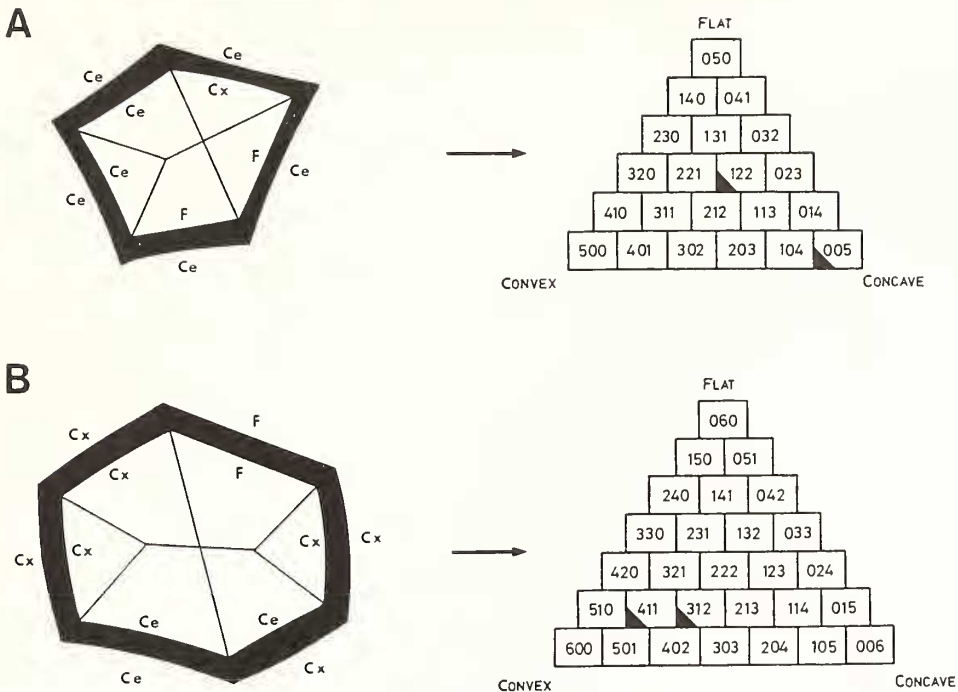
TEXT-FIG. 6. The definition of corallite shape in *Hexaphyllia*. The shape of any corallite is determined by two ratios, an inner wall shape ratio and an outer wall shape ratio. The number of wall sections that are respectively convex (Cx), flat (F) and concave (Ce) is defined by each ratio. Pyramid diagrams can then be used to plot the wall shape ratios for any given number of corallites. In the examples illustrated both inner and outer wall shape ratios are plotted on the same pyramid diagram – although they are usually plotted separately (see Text-fig. 7). A, corallites with five septa, an inner wall shape ratio of 1:2:2 and an outer wall shape ratio of 0:0:5.
    B, corallites with six septa, an inner wall shape ratio of 3:1:2 and an outer wall shape ratio of 4:1:1.

since, in an assemblage of fragmented corallites, specimens in the 1·2–1·3 mm diameter range and representing the earlier stages in growth of the larger individuals, would still be expected. The explanation favoured here for the bimodal distribution is that corallites in the 1·2–1·3 mm diameter range were selectively removed by currents. The same process may also explain how corallites became aligned parallel to the strike of the algal reef and had most of their spines removed.

Spine spacing and tabulae spacing. Reference to Text-figures 4 and 10 indicates that as corallite size increases, so do the spacing distances of tabulae and spines. In corallites of the same size, the variation in both parameters is both wide and continuous. In 1·2 mm diameter corallites for example, the tabulae spacing value ranges from 0·2–2·3 mm and the spine spacing distance from 1·0–1·8 mm. In addition, the spacing between tabulae is significantly higher in corallites from the fore-reef than in those from the algal reef (Pl. 3, figs 5, 8).
    The differences in tabulae spacing, wall thickness and shape noted above, reflect morphological adaptations to life at different positions within the reef caused by differences in growth rate and changes in the shape of the polyps' calicoblast layer during the skeletal secretion. These differences in turn reflect a response to variations in water depth, turbulence, the rate at which corallites settled in the sediment, sedimentation rate, or, a combination of these factors. Further details relating to the morphological differences between the two assemblages are discussed in detail elsewhere (Cossey 1983).
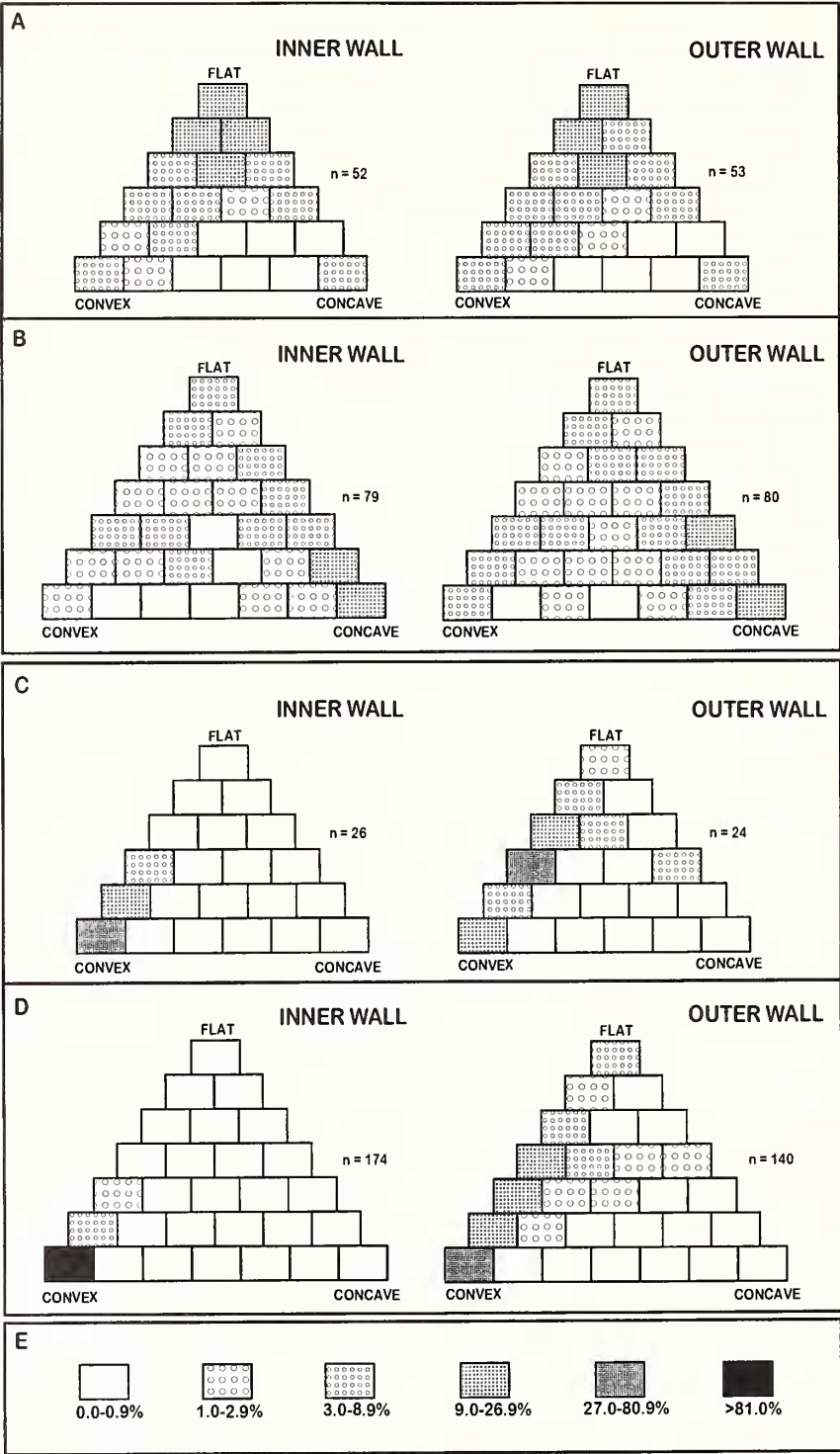
TEXT-FIG. 7. For caption see opposite.

SYSTEMATIC PALAEONTOLOGY

Order HETEROCORALLIA Schindewolf, 1941
Family HETEROPHYLLIIDAE Dybowski, 1873

Genus HEXAPHYLLIA Stuckenberg, 1904

Type species. Hexaphyllia prismatica Stuckenberg, 1904 (p. 72, pl. 3, fig. 5a–d) from the Lower Carboniferous of central Russia.

Emended diagnosis. Elongate, cylindrical or prismatic heterocorals with up to six sides and a maximum of six septa which meet at or near the axis. The peripheral edges of the septa may thicken and project through the wall to form longitudinal ridges or costae along the side of the corallite. The costae may be adorned with tubercles or spines which curve distally in the direction of corallite growth. Whilst the internal structure of the costae, spines and tubercles appears to be continuous with the septa, their external structure appears to form an extension of the tabulotheca. The tabulae are complete and slightly domed structures near the axis, but turn downwards peripherally and fuse together between the distal edges of the septa to form the tabulotheca. Corallite diameters and tabulae spacing values are continuously variable parameters.

Remarks. The genus was erected for those heterocorals possessing only six septa and was based on *Hexaphyllia prismatica* from central Russia. Later, Poty (1978*a*, 1981) demonstrated that some heterocorals with six septa were simply juveniles of the multiseptate *Heterophyllia* and more recently, Rodriguez and Comas-Rengifo (1989) described populations of *Hexaphyllia*? in which the number of septa ranged from four to ten, but six-septal forms predominated. For such reasons the validity of the genus *Hexaphyllia* was questioned by Rodriguez and Comas-Rengifo (1989) and Fedorowski (1991). With the exception of a single specimen of *Heterophyllia ornata* (see Pl. 2, fig. 8) none of the remaining 1300 corallites from Castleton possessed more than six septa. In view of this and because six-septal forms are the norm, representing more than 80 per cent. of both assemblages, the generic status of *Hexaphyllia* is upheld in this account. Although the presence of spines in both *Heterophyllia* (Pl. 2, fig. 8; Pl. 3, fig. 1) and *Hexaphyllia* (Pl. 1) may indicate a closer relationship than previously suspected, the exact systematic relationship between the two genera remains unclear.

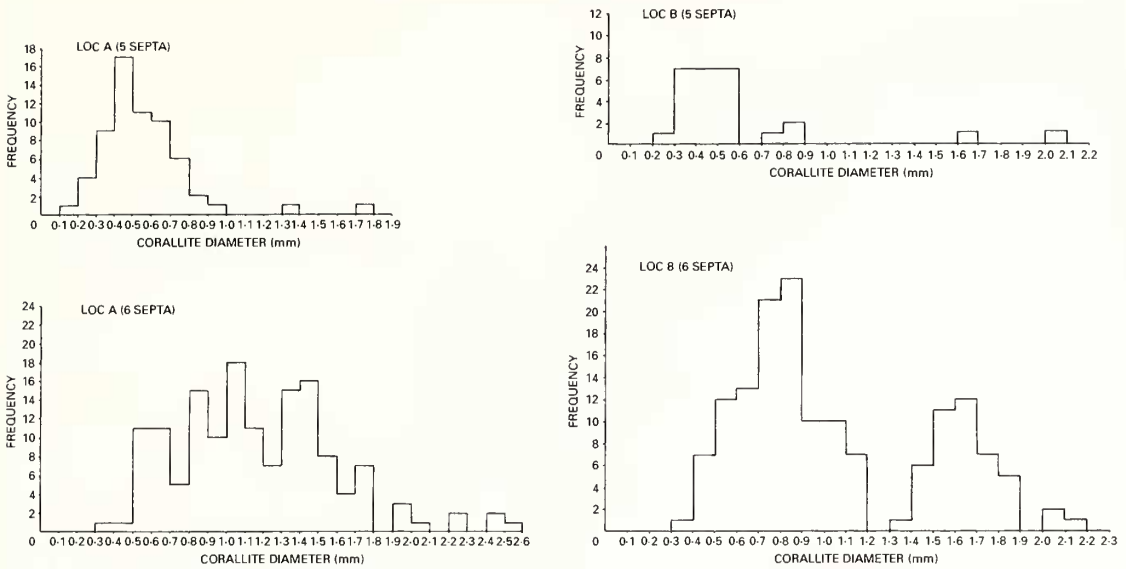### *Hexaphyllia marginata* (Fleming, 1828) emend.

Plate 1, figures 1–8; Plate 2, figures 1–7; Plate 3, figures 2–15; Text-figure 11A–D

|	
1828	*Lithostrotion marginatum* Fleming, p. 508.
1844	*Serpula hexicarinata* M'Coy, p. 169, pl. 23, fig. 28.
1867	*Heterophyllia M'Coyi* Duncan, p. 645, pl. 31, fig. 3a–c.
1867	*Heterophyllia Lyelli* Duncan, p. 646, pl. 31, fig. 4a–c.
1867	*Heterophyllia mirabilis* Duncan, p. 646, pl. 31, figs 5a–h.
1904	*Hexaphyllia prismatica* Stuckenberg, p. 72, pl. 3, fig. 5a–d.
1917	*Hexaphyllia mirabilis* (Duncan); Robinson, p. 178.
1939	*Hexaphyllia elegans* Yabe and Sugiyama, p. 500, pl. 26, figs 1–3; text-fig. 1.
1939	*Hexaphyllia japonica* Yabe and Sugiyama, p. 501, pl. 26, figs 1b–c, 4–5.
1971	*Hexaphyllia mirabilis* (Duncan); Mihaly, p. 54, pl. 1, figs 1–5; pl. 2, figs 1–3.
1975	*Hexaphyllia guangxiensis* Jia and Xu, p. 94, pl. 2, figs 5a–b.

TEXT-FIG. 7. Pyramid diagrams illustrating wall shape variations in corallites of *Hexaphyllia marginata* from the Castleton Reef Belt. A, corallites from the fore-reef (locality A) with five septa. B, corallites from the fore-reef (locality A) with six septa. C, corallites from the algal reef (locality B) with five septa. D, corallites from the algal reef (locality B) with six septa. E, scale – in which the number of corallites with a specific wall shape ratio is expressed as a percentage of the total number of corallites plotted in each diagram.
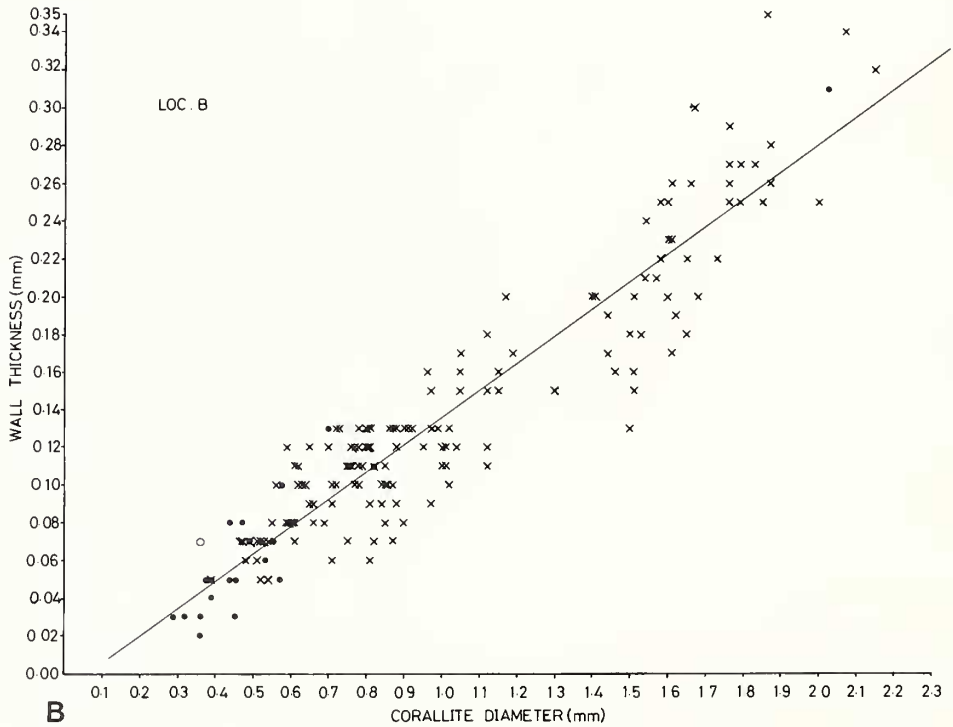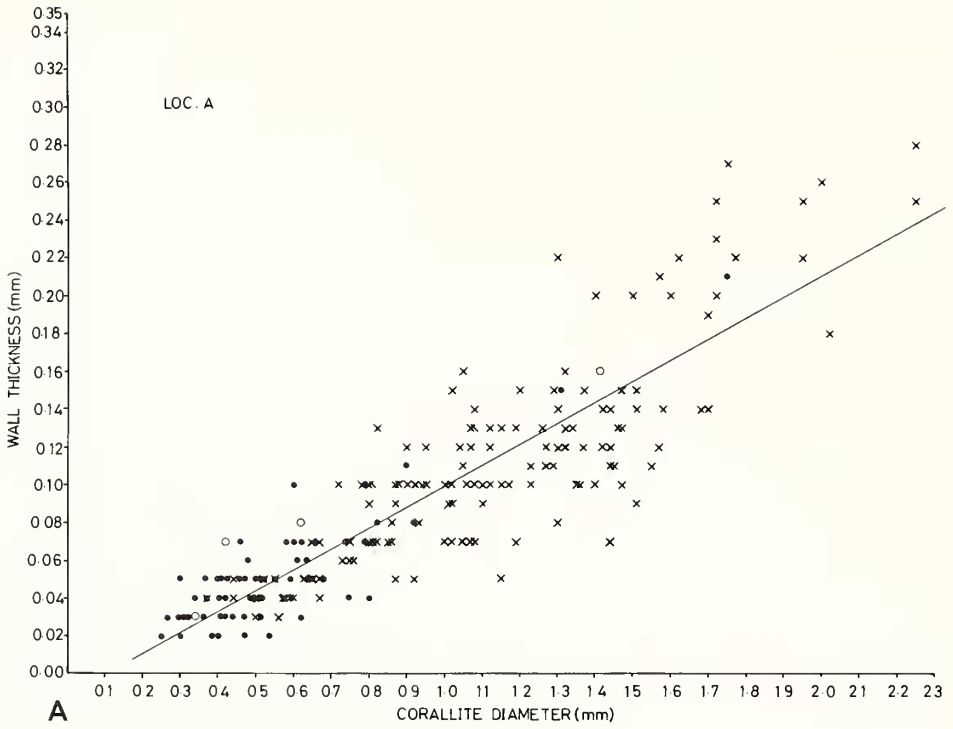
TEXT-FIG. 8. For caption see opposite.

TEXT-FIG. 9. *Hexaphyllia marginata* (Fleming, 1828) – size frequency plots. A, corallites from the fore-reef (locality A). B, corallites from the algal reef (locality B).
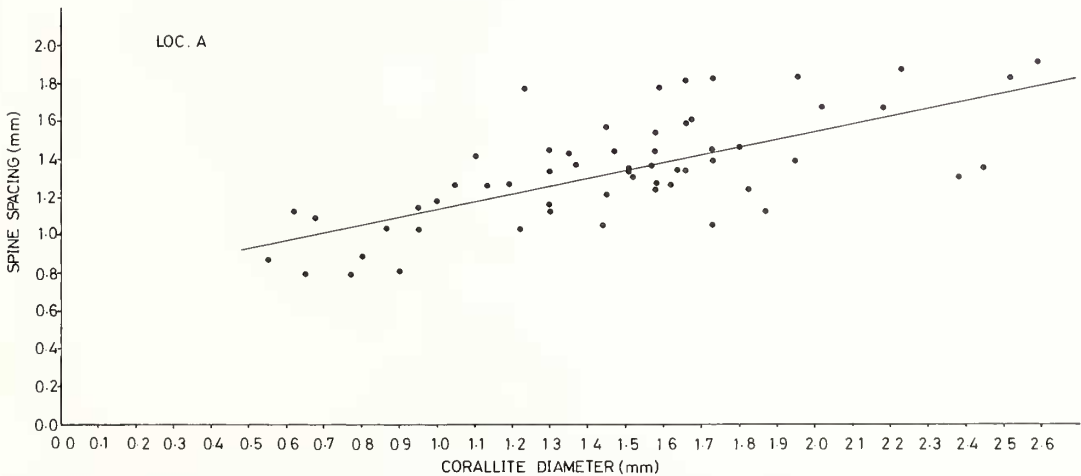
TEXT-FIG. 10. The relationship between corallite diameter and the spine spacing distance in corallites of *Hexaphyllia marginata* from the fore-reef (locality A).

1977	*Hexaphyllia zhongguoensis* Xu; Jia *et al.*, p. 243, pl. 60, fig. 9a–b.
1977	*Hexaphyllia guixiensis* Kuang; Jia *et al.*, p. 243, pl. 60, fig. 11a–b.
1978	*Hexaphyllia transversa* Yu, Lin, Huang and Cai, p. 47, pl. 14, figs 1a–b, 2–3; pl. 15, figs 5–6.
1978	*Hexaphyllia tenuis* Yu, Lin, Huang and Cai, p. 49, pl. 14, figs 5a–b, 6–7.
1978	*Hexaphyllia elongata* Yu, Lin, Huang and Cai, p. 49, pl. 14, figs 12a–b, 13; pl. 15, fig. 7.

TEXT-FIG. 8. The relationship between corallite diameter and wall thickness in *Hexaphyllia marginata*. A, corallites from the fore-reef (locality A). B, corallites from the algal reef (locality B). Note how wall thickness increases at a greater rate in corallites from the algal reef. Circles – corallites with four septa; dots – corallites with five septa; crosses – corallites with six septa.

1980 *Hexaphyllia concavia* Metcalfe *et al.*, p. 25, pl. 3, figs 13, 15.
1980 *Hexaphyllia xizangensis* Wang, p. 43, pl. 1, figs 1–2.
1980 *Hexaphyllia quighaiensis* Wang, p. 43, pl. 1, fig. 3.
1980 *Hexaphyllia quilianshanensis* Wang, p. 44, pl. 1, fig. 7.
1980 *Hexaphyllia jiangdaensis* Wang, p. 45, pl. 1, fig. 11.
1981 *Hexaphyllia minor* Xu, p. 46, pl. 1, figs 8a–b, 9.
1981 *Hexaphyllia yangchunensis* Xu, p. 46, pl. 1, figs 10a–b, 11a–b
1981 *Hexaphyllia crassa* Xu, p. 46, pl. 1, figs 6, 7a–b.
1981 *Hexaphyllia marginata* Poty, p. 73, pl. 34, fig. 17.
1981 *Hexaphyllia mirabilis* Poty, p. 72, pl. 34, figs 15–16.
1984 *Hexaphyllia yabei* Sugiyama, p. 42, pl. 1, figs 1a–8b; pl. 2, figs 1a–4; pl. 4, figs 3–5; text-figs 4b, 9.
1984 *Hexaphyllia inflata* Sugiyama, p. 60, pl. 3, figs 1a–9; text-fig. 12.
1984 *Hexaphyllia forcipis* Wang and Ye, p. 34, pl. 6, fig. 3a–b.
1984 *Hexaphyllia majaiaobaensis* Wang and Ye, p. 35, pl. 6, fig. 5a–b.
1984 *Hexaphyllia tenuiformis* Wang and Ye, p. 34, pl. 6, fig. 6.
1985 *Hexaphyllia longlinensis* Lin and Wu, p. 273, pl. 1, figs 9a–b; 10; text-fig. 1.
1985 *Hexaphyllia tenuis longhuoensis* Lin and Wu, p. 273, pl. 1, figs 11a–b, 12–13.
1985 *Hexaphyllia gigantea crassotheca* Lin and Wu, p. 273, pl. 1, figs 7a–b, 8.
1986 *Hexaphyllia elegantula* Huang and Ma, p. 17, pl. 4, figs 1, 1a–b.
1986 *Hexaphyllia weiningensis* Huang and Ma, p. 15, pl. 3, fig. 1a–b.
1986 *Hexaphyllia irregulare* Huang and Ma, p. 16, pl. 3, fig. 14a–b.
1986 *Hexaphyllia hexagonae* Huang and Ma, p. 17, pl. 4, figs 8a–b, 9–10.
1986 *Hexaphyllia cylindrica* Huang and Ma, p. 17, pl. 4, figs 12a–b, 13a–b, 14.
1986 *Hexaphyllia curta* Huang and Ma, p. 17, pl. 3, figs 19a–b, 20.
1986 *Hexaphyllia clina* Huang and Ma, p. 15, pl. 3, figs 4a–b, 5.
1992 *Hexaphyllia asymmetrica* Liu and Su, p. 476, pl. 1, fig. 1a–b.
1992 *Hexaphyllia extensa* Liu and Su, p. 477, pl. 1, fig. 3a–b.
1992 *Hexaphyllia spinalus* Lin, Huang, Wu, Peng and Qiu, p. 41, pl. 3, figs 1a–2b; text-fig. 1.44.
1992 *Hexaphyllia multitabulata* Lin, Huang, Wu, Peng and Qiu, p. 41, pl. 3, figs 3a–4b; text-fig. 1.45.
1992 *Hexaphyllia yui* Lin, Huang, Wu, Peng and Qiu, p. 43, pl. 3, fig. 8a–b; text-fig. 1.48.
1992 *Hexaphyllia flexus* Lin, Huang, Wu, Peng and Qiu, p. 44, pl. 3, fig. 7a–b; text-fig. 1.49.
1992 *Hexaphyllia crassotheca* Lin, Huang, Wu, Peng and Qiu, p. 44, pl. 3, figs 11–12; text-fig. 1.50.
1992 *Hexaphyllia fractiflexus* Lin, Huang, Wu, Peng and Qiu, p. 45, pl. 4, fig. 1a–b; text-fig. 1.51.
1992 *Hexaphyllia aboloformis* Lin, Huang, Wu, Peng and Qiu, p. 46, pl. 4, figs 2a–b; text-fig. 1.55.
1994 *Hexaphyllia lata* Lin and Yuan, p. 935, figs 2·5–2·6.

EXPLANATION OF PLATE 3

Figs 1–15. Heterocorals from the Lower Carboniferous, Castleton Reef Belt in North Derbyshire. All specimens are of Upper B_2 (Asbian) age.
Fig. 1. *Heterophyllia angulata* Duncan, 1867; USDES HCS 270; slopes of Middle Hill above Giants Hole; transverse thin section; × 10.
Figs 2–15. *Hexaphyllia marginata* (Fleming, 1828). 2–4, 6–8, 10–13 and 15, from the fore-reef at Winnats Pass (locality A). 2, MM LL10909k; juvenile corallite attached to adult, transverse peel-section; × 9. 3, MM LL10907a; six-septal form with spines, transverse peel section; × 6. 4, MM LL10907b; juvenile corallite attached to adult, transverse thin section; × 11. 6, MM LL10914a; corallite with four septa, transverse thin section; × 62. 7, MM LL10914a; five-septal form with spine, transverse thin section; × 37. 8, MM LL10909k; corallite with widely spaced tabulae, transverse peel section; × 23. 10, MM LL10917; corallite with four septa, transverse thin section; × 27. 11, MM LL10918a; five-septal form, transverse peel section; × 10. 12, MM LL10916; spiny corallite with six septa, transverse thin section; × 6. 13, MM LL10917; spiny six-septal form, transverse thin section; × 7. 15, MM LL10915a; transverse thin section; × 13. 5, 9, 14, from the algal reef at Treak Cliff (locality B). 5, MM LL10902b; corallite with closely spaced tabulae, longitudinal peel section; × 26. 9, MM LL10901a; corallites with three and five septa, transverse thin section; × 27. 14, MM LL10900b; transverse peel section; × 9.

PLATE 3

COSSEY, *Heterophyllia, Hexaphyllia*
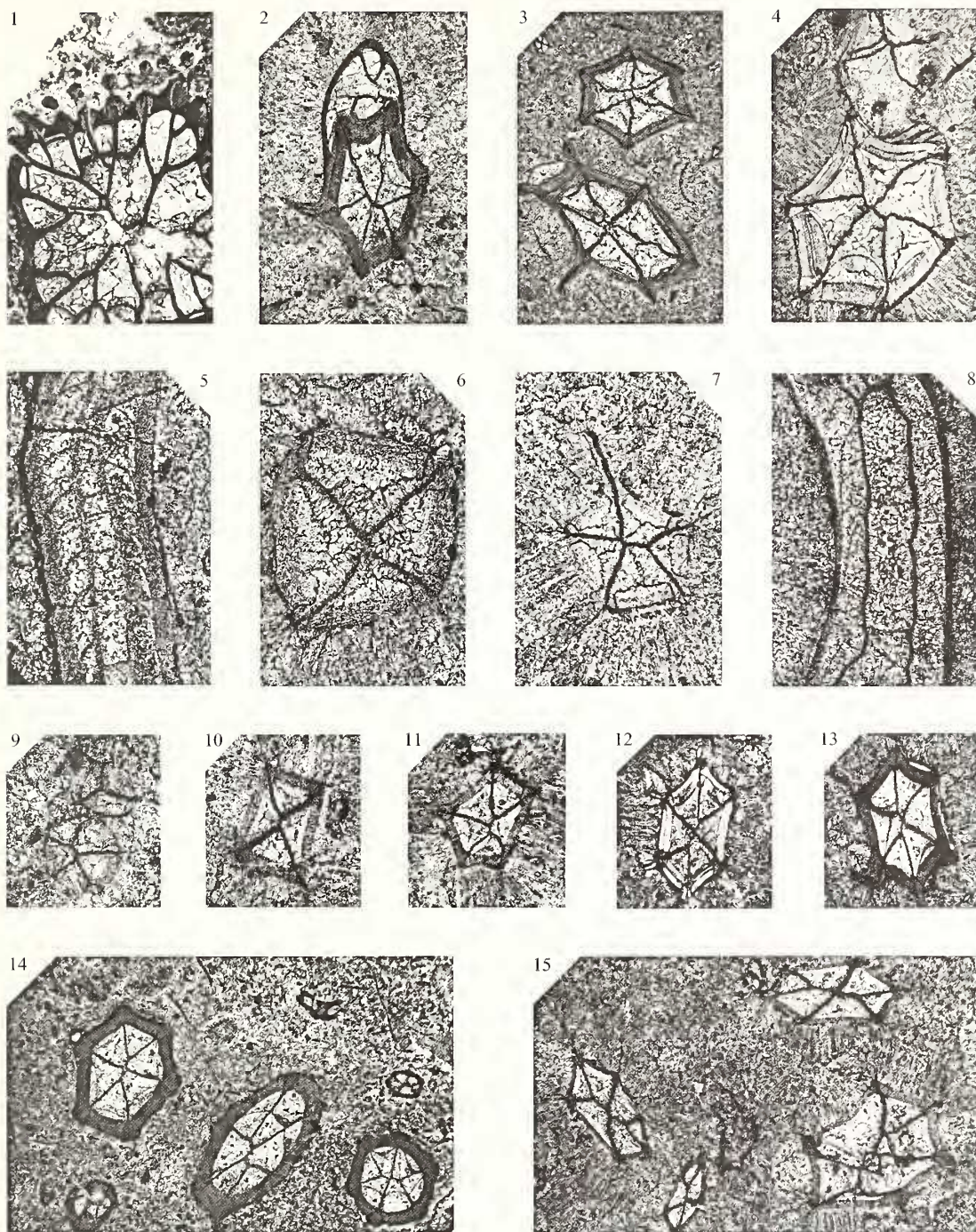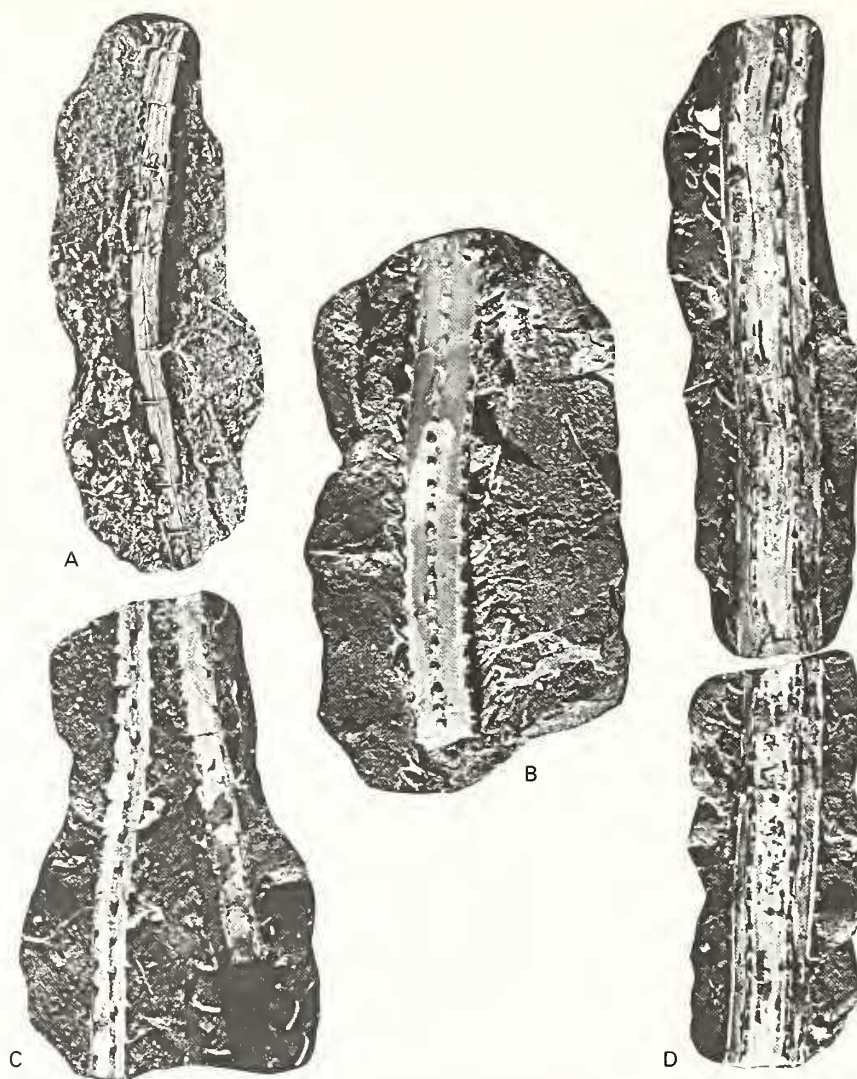
TEXT-FIG. 11. *Hexaphyllia marginata* (Fleming, 1828) from the Lower Carboniferous of Scotland. A, NMS G 1979.1.30; Petershill Formation, D_2 (Brigantian), near Bathgate, West Lothian; note that the wall is composed of overlapping plates (tabulae) resembling roof tiles; × 2·4. B–D, Lower Limestone Group, (Brigantian), Craigenglen, Campsie, near Glasgow. B, GLAMG 01-53cu (1·1); × 5. C, GLAMG 01-53cu (1·2); × 5. D, proposed neotype, GLAMG 01-53cu (2); × 5.

Type material. The type material of *Lithostrotion marginatum* Fleming 1828, and *Heterophyllia Lyelli*, *H. M'Coyi*, *H. mirabilis* of Duncan (1867) is untraceable (Hill 1938–41; Kato 1971; Khoa 1977). The type of *Serpula hexicarinata* (M'Coy, 1844) is inadequate for the revised concept of the species described in this account. A suggested neotype for *Hexaphyllia marginata* is GLAMG O1-53 cu (2) from the John Young Collection (Text-fig. 11D).

Additional material. Approximately 1300 corallites collected by the author from Lower Carboniferous (Asbian) reef limestones at Winnats Pass and Treak Cliff in the Castleton Reef Belt, North Derbyshire, England (Text-fig. 2), deposited at The Manchester Museum (MM); 70 corallites from the John Young Collection,

Kelvingrove Museum, now part of Glasgow Art Gallery and Museum (GLAMG); 15 corallites from the Hunterian Museum, Glasgow and ten corallites from the Horsfield Collection, Department of Earth Sciences, University of Sheffield (USDES); the type specimen of *Serpula hexicarinata* M'Coy, 1844, from the National Museum of Ireland, Dublin; the Jameson Collection in the Royal Museum of Scotland, Edinburgh (RSM); and other heterocoral collections from the Palaeontology Department, The Natural History Museum, London, and the British Geological Survey at Keyworth (Nottingham) and Edinburgh.

Emended diagnosis. As for the genus.

Description. The earliest stage in ontogeny is marked by an encrustation. The proximal end of each corallite forms an expanded 'talon-like' structure attached to an adult corallite of the same species. Septal insertion is initially rapid and difficult to define in the talon, and subsequently very slow. Typically, individuals have from three to six septa, the number of septa increasing with corallite size (Text-fig. 8). Although corallites with three to four septa are rare (Pl. 3, figs 6, 9–10), individuals with five to six septa (Pl. 3, figs 7, 9, 11–13) are very common. Corallite diameter ranges continuously from 0·1–2·6 mm. Corallites usually occur as fragments up to 89 mm long. Fragments are seldom perfectly straight and are often slightly sinuous (Pl. 1, fig. 1). Kinked corallites which show a dramatic changes in growth direction also occur (Pl. 1, fig. 3). The length of the unfragmented corallites is likely to have been considerable. Curved spines or tubercles (the abraded remnants of spines) may develop on the costae and are usually well spaced (Pl. 1, figs 1–2, 4; Text-fig. 10). Occasionally, two or three spines may issue from a common spine base (Pl. 2, fig. 7). Spines were recorded on corallites of all sizes from 0·25–2·59 mm including forms with four to six septa. Tabulae are domed and well-spaced along the corallite axis, but turn downwards peripherally and fuse together between the distal edges of the septa to form the thick wall structure. Tabulae spacing values range continuously from 0·2–3 mm (Text-fig. 4). Observation of transverse sections through the wall structure indicates that up to 12 tabulae may have fused together to form the tabulotheca (Text-fig. 3B–D; Pl. 2, figs 1–2, 4). Between the distal edges of the septa the shape of the wall is highly variable. Corallites may be stellate, prismatic or cylindrical in appearance according to whether the walls are respectively, either concave, flat or convex (Text-figs 6–7).

Remarks. The suggestion that *Heterophyllia lyelli* Duncan, 1867 and *H. m'coyi* Duncan, 1867 are species of *Hexaphyllia* was originally suggested by Stuckenberg (1904). Subsequently, another of Duncan's species, *H. mirabilis*, was transferred to the genus by Robinson (1917). Later, Hill (1938–41) identified *H. lyelli* (Duncan) as the junior subjective synonym of *Lithostrotion marginatum* Fleming.

Large numbers of *Hexaphyllia* species have since been described, particularly from China (Jia and Xu 1975; Jia *et al.* 1977; Yu *et al.* 1978; Wang 1980; Xu 1981; Wang and Ye 1984; Lin and Wu 1985; Huang and Ma 1986; Lin *et al.* 1992; Liu and Su 1992; Lin and Yuan 1994), where the recognition of different taxa is based on subtle differences in morphology and where intraspecific variation appears not to have been considered. Criteria used in the definition of *Hexaphyllia* species include: the presence or absence of spines or tubercles; wall thickness and shape; corallite diameter; the shape of the costae; the density of tabulae along the corallite axis.

Intraspecific variation in Heterocorallia was first noted by Young (1868, 1869) who demonstrated convincingly the synonymy of *H. lyelli* and *H. mirabilis* of Duncan (1867). Duncan's original descriptions suggested that *H. mirabilis* had a corallite diameter of 1 mm, the tabulae were widely spaced, the walls slightly convex, occasionally concave and the costae narrow but commonly adorned with spines or tubercles, and that *H. lyelli* had a corallite diameter of 2·5 mm, the spacing between the tabulae was 'average', the walls slightly concave and the costae large but with only occasional tubercles, pits and grooves. Young (1868) examined heterocorals from the same locality as Duncan and found corallites ranging in diameter from 0·6–2·5 mm, with one corallite tapering from 1·3–2·5 mm along its length. He also demonstrated that corallites of all diameters from 0·6–2·0 mm possessed spines and that the tubercles were merely eroded spine remnants. In addition, wall shape and tabulae spacing were seen to be highly variable.

In recent years, intraspecific variation in *Hexaphyllia* populations has become more widely recognized. Fontaine *et al.* (1991) described significant variations in wall shape, and considerable differences in corallite diameter have been recorded by other workers (Poty 1978*a*, 1981; Herbig

1986; Rodriguez and Comas-Rengifo 1989). Additionally, Sugiyama (1984) noticed significant variations in tabulae spacing and corallite diameter.

In this account, a wide and continuous range in corallite morphology has been demonstrated in both *Hexaphyllia* populations described from the Castleton Reef Belt. Corallite diameters range from 0·1–2·6 mm and, if corallites from the J. Young Collection are considered, this range is extended up to 3·9 mm. Spines occur on corallites of all sizes from 0·25–2·6 mm and the spacing between tabulae ranges from 0·2–3·0 mm. The presence or absence of spines or tubercles, or differences in size or shape of the costae, is attributed to the effects of pre-burial erosion. Corallite shapes vary and may be either cylindrical, prismatic or stellate according to whether the walls are predominantly either convex, flat or concave. As a result, corallites from both assemblages in the reef belt are regarded as variants of a single species and, since many previously described *Hexaphyllia* species fall within the limits of variation described in the Castleton material, the synonymy list in this account is extensive, including as many as 51 pre-existing taxa. Most of the criteria used to distinguish *Hexaphyllia* species in the past are therefore thought to be invalid.

This work supports the original conclusions of Young (1868, 1869) and echoes the sentiments expressed by Fontaine *et al.* (1991, p. 66) who stated that in all probability far 'too many species of *Hexaphyllia* have been recognized'.

MODE OF LIFE AND FUNCTIONAL MORPHOLOGY

Reference to the literature indicates that heterocoral mode of life is incompletely comprehended. The debate so far has centred upon the extent to which the heterocorals may have been either pseudoplanktic or benthic at different stages in their life, and how they may or may not have been attached to different substrates in either of these two situations. In order that the group may be better understood, details regarding their geographical distribution, functional morphology and facies associations have to be considered.

The earliest reference to heterocoral mode of life was made by Schindewolf (1941) who suggested that, on the basis of their scattered distribution, corallite length and the presence of spines in some species, the Carboniferous genera *Heterophyllia* and *Hexaphyllia* led a pseudoplanktic existence attached to seaweeds. Later, Rózkowska (1969) reasoned that heavily built taxa possessing 'talons' (e.g. *Oligophylloides*) were likely to be part of the sessile benthos. The idea that *all* heterocorals were benthic during their adult life was originally proposed by Cossey (1983). In developing this view, Sugiyama (1984, 1989) argued for the existence of two separate benthic groups (one 'attached' and the other 'sessile'), the two being distinguished from one another on the basis of whether or not the septa projected through the corallite wall and carried spines. Forms with septa penetrating the wall (e.g. *Heterophyllia*, *Hexaphyllia* and *Pentaphyllia*) were assumed to have been 'attached' by the cementing tips of spines to hard objects, such as rocks, shells, other heterocorals or dendroid rugose corals. Other genera that lacked wall-penetrating septa and spines (e.g. *Radiciphyllia* and *Oligophylloides*) were presumed to have been cemented directly to the sea floor by talon-like attachments. More recently, Lin, Wu and Qiu (1992) suggested that some heterocorals might even have been nektic in habit although supporting evidence for this assertion is unclear.

Functionally, the heterocorals appear to have been much better suited to a benthic rather than a planktic mode of life. In shallow surface waters their lengthy, delicate and sometimes highly ornamented corallites would have been prone to fragmentation. They were, however, well adapted to life in relatively quiet, low energy environments, where the degree of turbulence and sedimentation rates were, for much of the time, very low.

A common characteristic of the group is that corallites are often sinuous (Pl. 1, fig. 1). In an earlier work the author argued that sinuosity developed as corallites re-oriented themselves by settling unevenly in soft sediment (Cossey 1983). More rarely, corallites occur in which sharp changes in the growth direction are apparent (Pl. 1, fig. 3). These geniculated or kinked corallites were probably produced as corallites re-oriented themselves after having been toppled or fragmented on the sea floor. A benthic mode of life may also account for the subtle differences in
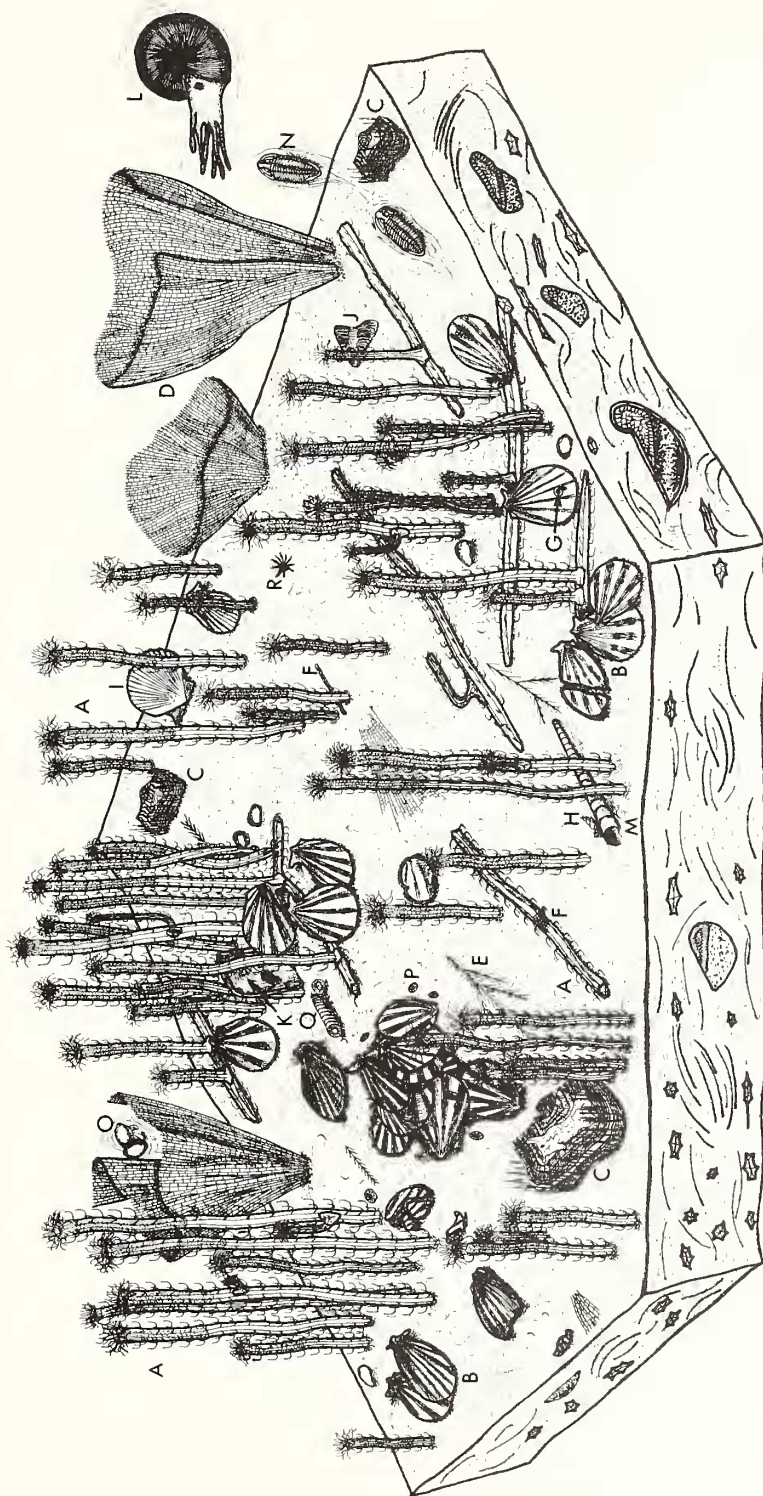
TEXT-FIG. 12. Reconstruction of the *Hexaphyllia* community from the fore-reef (locality A). A, *Hexaphyllia marginata*; B, *Streblochondria elliptica*; C, buxtoniids; D, *Fenestella*; E, *Penniretepora*; F, assorted bryozoa including encrusting forms; G, spirorbid; H, gastropod; I, *Aviculopecten*; J, *Leiopteria*; K, *Pinna*; L, *Bollandoceras*; M, orthoconic nautiloid; N, *Cunningella*; O, *Entomoconchus*; P, *Cyclus radialis*; Q, pelmatozoan fragments; R, *Claviradix*.
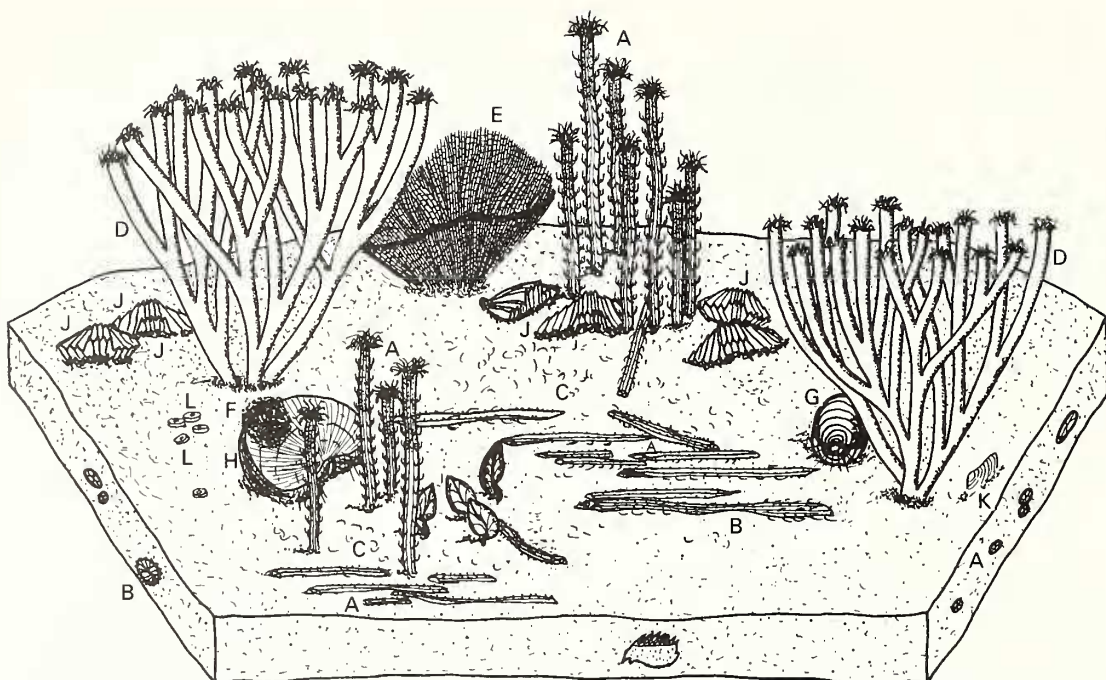
TEXT-FIG. 13. Reconstruction of the *Hexaphyllia* community from the algal reef (locality B). A, *Hexaphyllia marginata*; B, *Heterophyllia ornata*; C, heterocoral spines; D, *Siphonodendron*; E, *Fenestella*; F, *Fistulipora*; G, *Acanthoplecta mesoloba*; H, *Linoprotonia*; I, *Dielasma*; J, rhynchonellids; K, *Parallelodon*; L, pelmatozoan ossicles. Note that both of the reconstructions illustrated (Text-figs 12–13) are based on the assumption that the fauna recorded from each locality was transported only a short distance from its place of origin.

morphology between the two heterocoral populations described in this account, in which corallites from the algal reef are more cylindrical, have thicker walls, fewer spines and more abundant tabulae than those of the fore-reef. These differences reflect the adaptational responses of the two coeval populations living at different positions within the reef where the degree of water circulation, turbulence and sedimentation rates may have varied considerably. The stouter, cylindrical corallites of the algal reef were stronger and better able to withstand the more turbulent conditions close to the reef crest than those thinner-walled, prismatic and stellate corallites living farther down the reef slope where conditions were much quieter (Text-figs 12–13).

A benthic mode of life is further confirmed by the occurrence of branching forms and weakly colonial coralla. Examples include *Anomalophyllia* from the Namurian Ardengost Limestone, in the Hautes-Pyrénées (Tourneur *et al.* in press), *Stellaphyllia* from the Eifelian Santa Lucia Formation, in northern Spain (Tourneur and Herrmann in press) and most notably in *Oligophylloides* from the Famennian of the Anti-Atlas, Morocco (Weyer 1995b). The development of a dense heavy colony is clearly typical of a benthic organism rather than a planktic one.

Attachment structures

Spines. In this account it has been suggested that the primary function of heterocoral spines was to afford protection to the exposed polyp at the growing end of the corallite. The suggestion that the spines could have been used for clinging on to floating seaweed (Schindewolf 1941) cannot be supported as they are non-articulating (see Young 1868, 1869), open arc-shaped structures of regular geometry. This situation appears in striking contrast to the epiplanktic *Cyathaxonia tantilla* where attachment to algae in the plankton is facilitated by development of planispirally coiled

protocoralla during early growth (Sando 1977). The spines of heterocorals were therefore quite clearly inappropriate for clinging on to any floating object. Furthermore, there is no direct evidence to support the view of Sugiyama (1984, 1989) that the heterocorals were attached to various objects on the sea floor by the 'cementing tips' of their spines. If the spines were used for attachment in this way, modified spine shapes and attachment scars would be expected, but so far features of this kind have not been described.

Talons. To date, the only positive evidence of heterocoral attachment structures comes in the form of basal and lateral talons. Basal talons formed early in the ontogeny of juvenile corallites following the settlement of larvae on a variety of hard substrates. Although originally described by Rózkowska (1969) in *Oligophylloides* from the Upper Devonian of Poland, these structures have since been documented in both *Mariaephyllia* and *Oligophylloides* attached to an assortment of 'dead' shelly material (including the remains of ammonoids, orthoconic nautiloids, bivalves and pelmatozoan stems) from strata of a similar age in Germany (Weyer 1995a, 1995b). Further examples, in *Hexaphyllia*, have been illustrated herein.

So far it has been assumed that basal talons were formed initially on hard, non-living substrates and primarily on shell debris that had been deposited on the sea floor. Whilst this certainly appears to be true in the majority of circumstances, it has to be questioned whether such initial attachments could have been made to substrates that were either: hard or soft, alive or dead, floating as part of the plankton, or swimming as part of the nekton. If, with further work, this latter circumstance proves to be the case, then it could help to explain not only the widespread distribution of the group, but also their occurrence in such a wide variety of different sedimentary facies. Rich heterocoral assemblages in pockets within reefs could then be regarded as originating from epiplanktic juveniles attached to drifted material washed into reef cavities, either as a single event in the case of an aggregate of drifted material, or over a period of time in the case of isolated associations. A somewhat similar explanation for the occurrence of rich goniatite assemblages in the Castleton Reef Belt was given by Ford (1965). If, however, as Weyer (1995a, 1995b) suggested, heterocorals occur only rarely in aphotic environments, this would preclude their membership as part of the plankton (whether attached or not) during adult life. It is therefore clear that heterocorals inhabited areas of deep water on the ocean floor as well as protected areas within shallow water reef systems and that their occurrence in reefs may be linked to the distribution of sheltered reef cavities.

Regardless of where their basal talons were formed, it is clear from the earlier discussion that the heterocorals were benthic during their adult life and that corallites grew upwards, away from the sediment-water interface at a high angle. Confirmation of this is provided in the form of rhodophyte encrustations. For example, Termier *et al.* (1975, fig. 17) illustrated *Aoujgalia variabilis* encrusting a *Hexaphyllia* corallite on all six sides, and Brady (1876, text-fig. 9) illustrated an encrustation of *Stacheia* which appears to encircle completely a corallite resembling *Heterophyllia*. Such circum-corallite encrustations are unlikely to have occurred unless the corallites were protruding from the sediment at a considerable angle.

Besides 'basal talons', the only other convincing attachment structures to be described in heterocorals are those referred to as 'lateral talons', described by Weyer (1995b, but see also 1995a) in *Oligophylloides tenuicinctus* and *Mariaephyllia* aff. *famenniana* from the Upper Devonian of Germany. These structures developed in corallites which grew beyond the juvenile stage and consist of bulbous projections from the corallite wall which terminate distally with distinctive flat surfaces. Weyer noted the association of these heterocorals with dysphotic cephalopod-rich limestones and suggested that lateral talons represented outgrowths of the corallite wall that were attached to the flat surfaces of benthic rhodophyte thalli growing in deep-water meadows. Although such structures have not so far been recorded in *Hexaphyllia*, Weyer's view confirms the idea that heterocorals were benthic forms that grew upright on the sea floor. Corallites would then have been supported by the slow accumulation of sediment around their base, by subsiding gradually into the sediment (which may explain the sinuous shape of many corallites), or by thickets of algae to which they may have been attached by lateral talons. In connection with the last of these, it is interesting

to note that in a reconstruction of Viséan upper reef slope communities from Yorkshire, Mundy (*in* Ramsbottom 1978) illustrated *Hexaphyllia* supported on the sea floor by conjectured vegetation, despite orientating the corallites incorrectly.

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